# AMBEDUS PUSILLUS, NEW GENUS, NEW SPECIES, A SMALL DIADECTID (TETRAPODA: DIADECTOMORPHA) FROM THE LOWER PERMIAN OF OHIO, WITH A CONSIDERATION OF DIADECTOMORPH PHYLOGENY

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## ABSTRACT

*Ambedus pusillus*, new genus, new species, is a small diadectid from the Lower Permian Greene Formation of Ohio that is distinguishable from all other members of the group by the presence of conical anterior teeth of the maxilla and dentary, high maxillary and mandibular tooth counts, a lesser degree of molarization of the cheek teeth, a shallow dentary, lack of a labial parapet, and a relatively shallow alveolar shelf that suggests a more shallow tooth implantation than that of other diadectids. The recognition of *A. pusillus* as a member of Diadectidae is supported by the presence of a heterodont dentition that possesses transversely expanded, molariform cheek teeth bearing: 1) a central cusp flanked by labial and lingual shoulders; and 2) wear facets developing on the lingual and labial shoulders of the maxillary and dentary cheek teeth, respectively. Although lacking a deep lower jaw, which is characteristic of herbivores and found in other diadectids, the presence of procumbent anterior teeth, molariform cheek teeth, and wear facets similar to those of other diadectids suggest that *Ambedus*, like all other diadectids, may have been herbivorous. Phylogenetic analysis of Diadectomorpha confirms its status as a natural group, and it supports both the monophyly of Diadectidae and the sister-group relationship of Diadectidae to *Tseajaia*. The recognition of *Limnoscelis* as the sister-taxon to *Tseajaia* + Diadectidae is also supported. Within Diadectidae, *Ambedus* is the sister-taxon to all other diadectids, with *Orobates*, *Desmatodon*, and *Diasparactus* + *Diadectes* representing progressively more derived taxa in a series of nested clades. With a greater species-richness and wider geographic range relative to other diadectomorph taxa, it is hypothesized that the evolution of herbivory in Diadectidae led to an evolutionary radiation of species within the group.

KEY WORDS:   Diadectidae, *Ambedus*, Diadectomorpha, Tetrapoda, Greene Formation, Dunkard Group, Permian, herbivory

## INTRODUCTION

The name Diadectidae was first proposed by Cope (1880a) to include the genera *Diadectes* and *Empedocles*, and within fifteen years of its description (Cope 1880b), nine additional genera were referred to the group. After significant taxonomic revisions (e.g., Case 1911; Olson 1947), six diadectid genera are currently recognized: *Phanerosaurus* Meyer, 1860; *Diadectes* Cope, 1878; *Stephanospondylus* (Geinitz and Deichmuller 1882); *Desmatodon* Case, 1908; *Diasparactus* Case, 1910; and *Orobates* Berman et al. 2004. *Desmatodon* is a Late Pennsylvanian taxon known primarily from skull material and dentition produced from the Missourian Red Knob Formation of Pennsylvania (Case 1908; Romer 1952; Berman and Sumida 1995), Missourian Sangre de Cristo Formation of Colorado (Vaughn 1969; Berman and Sumida 1995), and Virgilian Cutler Formation of New Mexico (Berman 1993). *Diasparactus* remains have been recovered from the Upper Pennsylvanian Virgilian Cutler and Ada formations of New Mexico and Oklahoma, respectively (Berman 1993; Kissel and Lehman 2002). The best known diadectid, *Diadectes*, is known from the Lower Permian of Colorado, New Mexico, Ohio, Oklahoma, Texas, Utah, West Virginia, Prince Edward Island, and Germany (Olson 1947; Langston 1963; Lewis and Vaughn 1965; Olson 1967; Berman 1971; Olson 1975; Berman 1993; Berman et al. 1998a), and *Phanerosaurus, Stephanospondylus*, and *Orobates* are

restricted to the Lower Permian of Germany (Berman et al. 1998a; Kissel et al. 2002; Berman et al. 2004). Reisz and Sutherland (2001) described a small collection of diadectid remains, including four frontals, one postfrontal, and 14 isolated teeth, that were collected from the Lower Permian near Richards Spur, Oklahoma. With the skull elements resembling those of *Diadectes absitus* and the dentition resembling that of *Orobates*, Reisz and Sutherland (2001) could not demonstrate that the Richards Spur diadectid elements are assignable to a single taxon, so a generic assignment of the material was considered premature, and the material remains unnamed.

Presented here is a new genus and species of Diadectidae from the Dunkard Group of Ohio. Collection data indicates that the specimens attributed to this new form, which was initially reported by Kissel and Reisz (2003), had been recovered from Clark Hill in Monroe County, Ohio, with the fossil-bearing horizon found approximately 8 feet (2.5 m) below the Nineveh Coal of the Greene Formation. The fossil remains are preserved in a light gray, micaceous claystone that weathers to tan. Remains of the dipnoan *Sagenodus*, the trimerorhachid *Trimerorhachis*, a possible embolomere, and the synapsid *Ctenospondylus ninevehensis* have also been reported from Clark Hill (Berman 1978). Produced from a single site in the Greene Formation, these four taxa were recovered from the Nineveh Limestone, which is interpreted as

a freshwater pond or lake deposit (Berman 1978). Recognition of the new form from Clark Hill marks only the second recorded occurrence of diadectid remains from Ohio and the third recorded occurrence of diadectid remains from the Dunkard. Olson (1970; 1975) reported the presence of *Diadectes* from the Belpre locality of Washington County, Ohio, and Berman (1971) referred a skull that was recovered from Roane County, West Virginia to *Diadectes*. With both the Belpre and Roane County localities found within the Washington Formation, the unit that underlies the Greene Formation, the new form represents the youngest diadectid recovered from the Dunkard. Age assignments of the Dunkard Group range from Late Pennsylvanian (e.g., Clendening 1975) to Early Permian (e.g., Durden 1975; Eagar 1975; Remy 1975), with the vertebrate taxa identified from Dunkard strata indicative of an Early Permian age (e.g., Berman and Berman 1975; Lund 1975; Olson 1975).

The purpose of this study is to describe this new genus and species of Diadectidae and examine its phylogenetic position within Diadectomorpha. When discussing characters of previously published phylogenetic analyses, the character numbers listed correspond to those assigned by the original authors.

## INSTITUTIONAL ABBREVIATIONS

CM—Carnegie Museum of Natural History, Pittsburgh, Pennsylvania

FMNH UC—Field Museum of Natural History, Chicago, Illinois

MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts

MNG—Museum der Natur, Gotha, Germany

OMNH—Sam Noble Oklahoma Museum of Natural History, Norman

UCMP—University of California Museum of Paleontology, Berkeley

YPM—Yale Peabody Museum, New Haven, Connecticut

## SYSTEMATIC PALEONTOLOGY

Cotylosauria Cope, 1880a
Diadectommorpha Watson, 1917
Diadectidae Cope, 1880a
*Ambedus*, **new genus**

*Diagnosis.*—A small diadectid distinguishable from other members of the group by: 1) a shallow dentary; 2) rela-

tively high maxillary and mandibular tooth count; 3) lack of a labial parapet of dentary; 4) anterior teeth of maxilla and dentary conical, in contrast to the incisiform anterior teeth of other diadectids; and 5) shallow alveolar shelf, which suggests a relatively shallow tooth implantation.

*Etymology.*—Latin, *ambedo*, to nibble.

*Ambedus pusillus*, new species
(Fig. 1–5)

*Holotype.*—MCZ 9436, nearly complete right maxilla.

*Horizon.*—Eight feet below Nineveh Coal Horizon, Greene Formation, Dunkard Group.

*Locality.*—Clark Hill, sec. 16, Salem Township, Monroe County, Ohio.

*Diagnosis.*—Same as that for the genus, this being the only known species.

*Referred Specimens.*—MCZ9437, poorly preserved maxilla; MCZ 9438, complete left dentary; MCZ 9439, anterior portion of right dentary; MCZ 9440, posterior portion of left dentary; MCZ 9441, poorly preserved dentary.

*Etymology.*—Latin, *ambedo*, to nibble; *pusillus*, tiny.

## DESCRIPTION AND COMPARISON

### *Introduction*

The material assigned to *Ambedus pusillus* consists of two maxillae (MCZ 9436 and 9437) and four dentaries (MCZ 9438, 9439, 9440, and 9441) of varying completeness. Both MCZ 9437 and 9441 are poorly preserved, with much of the bone either missing or severely damaged, so the description of *A. pusillus* is restricted to four elements, a right maxilla (MCZ 9436) and a left (MCZ 9438) and two right (MCZ 9439 and 9440) dentaries. MCZ 9436 is incomplete anteriorly and also lacks the extreme posterior tip, and MCZ 9439 and 9440 lack the posterior and anterior portions, respectively. In order to preserve the impression of the sixth tooth of the series, matrix was not completely prepared from the anterior portion of MCZ 9439; thus, the anterior teeth of this specimen are exposed in lateral view only. MCZ 9438 is a complete left dentary exposed primarily in lateral view, with the occlusal surfaces of several teeth also exposed. Prior to their recognition as diadectid remains, the above specimens were collectively catalogued as MCZ 8667 and assigned to *Mycterosaurus* sp. Also referred to MCZ 8667 is an isolated humerus that was collected within the same vicinity as the maxillae and dentaries. Because the humerus exhibits no features indicative of Diadectidae, it

is not referred to *Ambedus pusillus*, and it is therefore not described herein.

Among diadectid taxa, the maxilla and dentary are known in *Diadectes*, *Diasparactus*, *Desmatodon*, and *Orobates*. The genus *Phanerosaurus* is based solely on an articulated series of four presacral and two sacral vertebrae (Meyer 1860), so comparison to it is not useful for this study. *Stephanospondylus* is known from a wider range of elements, including tooth-bearing elements of the upper and lower jaws (Stappenbeck 1905; Romer 1925), but it remains a poorly known taxon, and Berman et al. (1998a) suggest that the holotype may represent a juvenile form. Further evaluation of this taxon is required, and it is therefore not included in this study unless specifically noted. Thus, comparison of *A. pusillis* is restricted primarily to *Diadectes*, *Diasparactus*, *Desmatodon*, and *Orobates*, with comparison to the Richards Spur diadectid material restricted to dental morphology.

As discussed below, the remains described herein as *A. pusillus* possess none of the features that typify known juvenile individuals of previously described diadectid taxa. All elements are therefore thought to represent those of adult individuals.

### Maxilla

The maxilla (Fig. 1) is represented by MCZ 9436, a nearly complete right maxilla that possesses 12 teeth and one empty alveolus. Only the extreme tip of the posterior end is lacking in MCZ 9436, but a larger portion of the anterior end is missing. Although the anterior portion of the tooth row is therefore likely incomplete in MCZ 9436, the preserved tooth positions are numbered from one to 13 for purposes of description, with tooth one representing the most anterior of the preserved teeth.

In lateral view, the dorsal margin is highly convex, as in the posterior region of the maxilla of both *Diadectes* and *Desmatodon*. The ventral margin is nearly horizontal, as in all diadectids. As preserved, the lateral surface is rough and pitted, but this texture no doubt results from poor preservation and crushing of the lateral surface, especially of the very thin dorsal lamina. With the exception of small foramina just above the tooth row, the lateral surface was likely smooth, as in the dentary, and it is flat and vertical. The dorsal portion of the dorsal lamina is displaced medially relative to the ventral portion of the lateral surface, but this displacement results from movement along a postmortem break that extends anteriorly from the posterior margin of the dorsal lamina to the level of the fifth tooth.

Description of the medial surface of the maxilla is restricted to the alveolar shelf, as the thin, fragile nature of the dorsal lamina prevented its complete preparation. The alveolar shelf is smoothly finished and, relative to other diadectids, shallow. It is a convex, rounded ridge to

the level of the fifth tooth. At the sixth tooth position, an arcuate groove originates from the ventral margin and extends to the ventral margin at the level of tooth ten. Anteriorly, the groove is wide and faces medially, but as it extends dorsoposteriorly, it narrows and faces dorsally and slightly medially. Posteriorly, the groove widens to form a dorsomedially facing platform. A ridge defines the dorsal margin of the groove anteriorly. Ventral to the groove, the alveolar shelf is convex. From the level of tooth five to tooth seven, the dorsal surface of the alveolar shelf is a flat, dorsally facing platform. It is slightly convex and faces dorsomedially throughout its remaining length.

MCZ 9436 possesses 13 teeth, including the empty alveolus at tooth position four. Because the anterior portion of MCZ 9436 is lacking, it can only be stated that a minimum of 13 maxillary teeth were present. In MCZ 9436, tooth 13 likely represents the last tooth of the maxillary series, so only the anteriormost maxillary teeth are not preserved. Maxillary tooth counts in other diadectids include 11 for *Diadectes* (Case and Williston 1912; Berman et al. 1998a), 12 for *Desmatodon* (Berman and Sumida 1995), 12 for *Orobates* (Berman et al. 2004), and the right maxilla of *Stephanospondylus* illustrated by Geinitz and Deichmüller (1882, plate IV, fig. 2) possesses a series of 12 teeth (Romer 1925).

The shallow alveolar shelf in *Ambedus pusillus* suggests that tooth implantation was not as deep as that in other diadectids. Whereas the root is longer than the height of the crown in *Diadectes*, *Diasparactus*, *Desmatodon*, and *Orobates*, the shallow alveolar shelf of MCZ 9436 indicates that root length is less than crown height in *Ambedus*, as observed in the diadectomorphs *Limnoscelis* and *Tseajaia*. In no specimen is it possible to determine if the marginal teeth of *Ambedus* exhibit infolding of the dentine, a feature present in all other diadectomorphs.

In occlusal view, the maxillary dentition is aligned in a straight row with only a slight lateral deflection anteriorly. It is possible that, if the tooth row were completely preserved, this deflection would continue and become more prominent, as in other diadectids. The maxillary dentition of heretofore known diadectids consists of two incisiform teeth that are succeeded by a series of molariform cheek teeth. The incisiform teeth are oval in section near the base and are excavated lingually on the distal half to produce a chisel-like distal tip, and the cheek teeth are transversely expanded with an occlusal surface that possesses a central cusp flanked by labial and lingual shoulders. The maxillary dentition of *Ambedus* adheres to this general pattern, but the anteriormost teeth of MCZ 9436 are not incisiform. Since the anterior portion is lacking in MCZ 9436, it is likely that the anterior teeth of the maxilla are also not preserved, opening the possibility that the anterior teeth, if present, would exhibit an incisiform morphology. However, the lack of incisiform anteri-
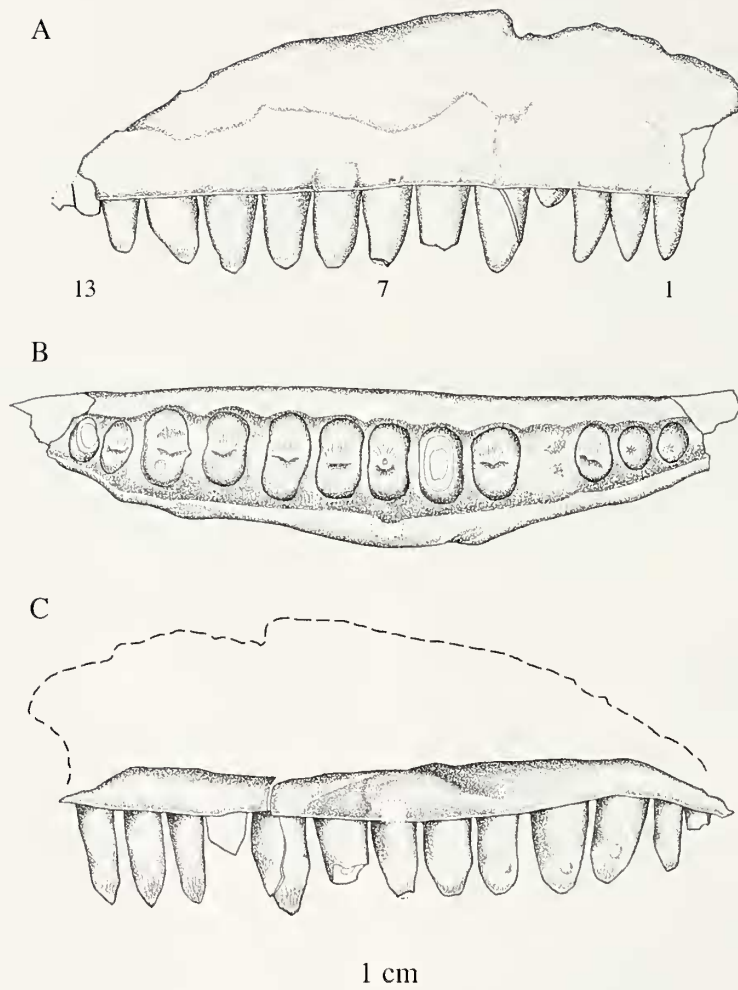
Fig. 1.—MCZ 9436, right maxilla and holotype of *Ambedus pusillus* in lateral (A), occlusal (B), and medial (C) views. Numbers indicate tooth positions.

or teeth on the dentary, as described below, strongly suggests that the upper tooth row also lacked incisiform dentition. As the tooth row in MCZ 9436 extends posteriorly, the teeth gradually expand transversely until tooth position nine, from which point they decrease in transverse width posteriorly to the end of the series. The alveolar shelf attains its greatest mediolateral width at the level of tooth seven in order to accommodate the transversely expanded cheek teeth. In *Diadectes*, the maxillary cheek teeth increase in width to the sixth or seventh tooth and then decrease to the posterior end of the series (Case and Williston 1912; Berman et al. 1998a). A similar pattern is found in CM 47654, a left maxilla of *Desmatodon hesperis*, but the serial decrease in width after the widest tooth, tooth seven, is less drastic than that in *Diadectes*.

The first two teeth of the maxillary series of *Ambedus pusillus* are conical with a weakly developed lingual shoulder and a medially directed central cusp.

Tooth three is the first of the series to exhibit the transversely expanded, molariform cheek teeth that are characteristic of diadectids, although the labial shoulder is weakly developed and the central cusp possesses a slight medial tilt. On teeth one to three, longitudinal fluting is present on the distal third of the lingual surface. Tooth four is not preserved. The fifth tooth possesses both labial and lingual shoulders, but the lingual shoulder is the larger of the two. Also, beginning with tooth five and present on the remaining teeth of the series, the central cusp is directed dorsally and longitudinal fluting is present on the distal half of the lingual surface and near the tip on the labial surface. Although tooth four is not present and tooth six is incomplete, they were likely intermediate in form between teeth three and five and five and seven, respectively.

Teeth seven to 11 possess a uniform morphology, with a low central cusp flanked by rounded shoulders

both labially and lingually, lacking the prominent labial and lingual cusps found in the cheek teeth of *Diasparactus* and all species of *Diadectes* except *D. absitus*. In *D. absitus*, the maxillary cheek teeth each bear a tall central cusp, and the labial and lingual cusps are poorly developed, resembling shoulders more than cusps (Berman et al. 1998a). The cheek teeth of *Desmatodon* possess well-developed central and lingual cusps, with a rounded shoulder labially.

With a nearly vertical labial surface and a medially sloping lingual surface near the base of the crown, the outline of the cheek teeth in posterior view (Fig. 2A) differs considerably from other diadectids. In *Orobates* and the unnamed Richards Spur diadectid, the cheek teeth exhibit an exaggerated teardrop, or spade-like, outline (Reisz and Sutherland 2001; Kissel et al. 2002), and *Diadectes*, *Diasparactus*, and *Desmatodon* exhibit abrupt, shoulder-like expansion of the labial and lingual margins dorsal to a slight constriction between the crown and root. Tooth nine of MCZ 9436 possesses the greatest transverse width of the series, and it also exhibits the greatest degree of molarization of the series. Berman and Sumida (1995) demonstrated that the cheek teeth in adult specimens of *Diadectes* possess a greater degree of molarization than those of adult *Desmatodon* specimens (i.e., the cheek teeth of *Diadectes* have a much greater transverse width relative to their anteroposterior length and dorsoventral height than those of *Desmatodon*). *Ambedus* possesses a similar degree of molarization as *Desmatodon hesperis* and a significantly lesser degree of molarization than both *Diadectes lentus* and *Desmatodon hollandi* (Table 1), with the similar height/width ratios exhibited by *A. pusillus* and *D. hesperis* resulting from the tall, well-developed central cusp of the latter species, in contrast to the low central cusp of the former, and not from a similarity in tooth morphology. Tooth 12 possesses a lesser degree of molarization than those teeth anterior to it, its morphology resembling tooth three. Only the base of tooth 13 is preserved, and it possesses a subcircular section.

Wear facets are present on the lingual shoulders of teeth nine, 10, and 11 in MCZ 9436. Such an uneven wear pattern of the maxillary cheek teeth, with a greater degree of wear on the lingual shoulder or cusp than on the labial shoulder or cusp, is characteristic of diadectids (Berman et al. 1998b). Of these wear facets, none possess microwear patterns (e.g., striations) that may indicate a direction, or directions, of jaw movement during oral processing.

## Dentary

The dentary (Figs. 3, 4, 5) is long and shallow, in strong contrast to that of all other diadectids in which the element is known. In *Diadectes* (Welles 1941; Berman et al. 1998a), *Desmatodon* (Berman and Sumida 1995),
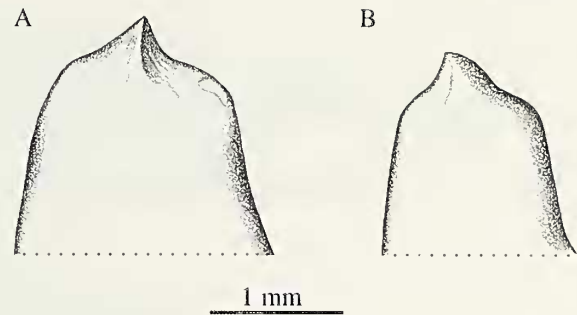


Fig. 2.—Fifth posteriormost maxillary tooth of MCZ 9436 (A) and fifth posteriormost dentary tooth of MCZ 9440 (B) in posterior view.

*Stephanospondylus* (Romer 1925), and likely *Diasparactus*, it is relatively short anteroposteriorly and deep dorsoventrally. The complete mandible of *Diasparactus* is known, but sutures delineating the individual elements are not visible (Case and Williston 1913); however, with the general morphology of the mandible and the known morphology of the dentary resembling that of *Diadectes* (Case and Williston 1913; Kissel and Lehman 2002), it is probable that the complete dentary of *Diasparactus* was similar to that of *Diadectes*.

Along the tooth-bearing area, the dorsal margin of the dentary of *Ambedus* is only slightly concave in lateral view. Posterior to the last tooth of the series, the margin is gently convex. In lateral view, the ventral margin is convex anteriorly and concave posteriorly. The ventral margin slopes posteroventrally, with the dentary possessing the greatest dorsoventral height posteriorly. In dorsal view, the dentary is thin anteriorly, expanding posteriorly to attain its greatest mediolateral width at tooth positions 14 and 15.

With the exception of several foramina and shallow, longitudinal grooves found below the tooth row, the lateral surface is smooth. In other diadectids, the lateral surface of the dentary is irregularly sculptured with prominent grooves and pits. Below the tooth row, the lateral surface, which is vertical in other diadectids, curves and continues as a flat surface that extends ventromedially, undercutting the alveolar shelf so that the ventral margin of the dentary lies medial to the tooth row in anterior view. The dentary lacks the labial parapet and associated groove that is found in *Diadectes*, *Diasparactus*, *Desmatodon*, and *Orobates*. Although initially described by Berman et al. (1998a) as lacking a labial parapet, further preparation of the holotype of *Diadectes absitus* (MNG 8853) has revealed the presence of a low parapet (D. S Berman, pers. comm.). In the paratype of *D. absitus* (MNG 8747), the right mandible is incompletely preserved, making determination of the presence of a labial parapet impossible, but it does possess a flat, dorsally facing platform lateral to the tooth row posteriorly (Berman
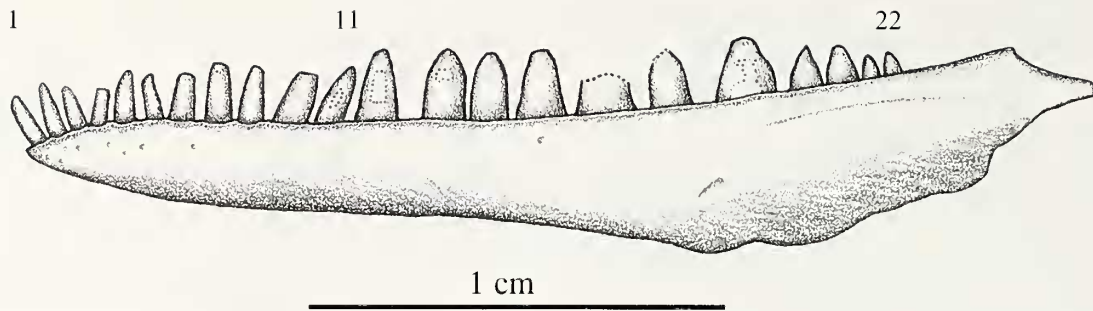
Fig. 3.—MCZ 9438, complete left dentary of *Ambedus pusillus* in lateral view. Numbers indicate tooth positions.

et al. 1998a), a feature also not present in *Ambedus*.

The medial surface of the dentary is traversed by a deep meckelian canal along its length. Anteriorly, the symphysis occupies the entire tip of the medial surface, extending posteriorly to the level of the third tooth. Its surface is rough and therefore distinct from the remaining medial surface. The meckelian canal continues anteriorly to divide the symphysis into distinct dorsal and ventral areas, leaving only a small area at the anterior tip of the symphysis to connect these two surfaces. The canal is shallowest within the symphysis, deepening and expanding dorsoventrally as it extends posteriorly. Dorsal to the canal, the medial surface of the dentary is convex from the symphysis to the level of the eighth tooth. Posterior to that position, the medial surface is flat and oriented vertically. Aside from a series of mostly longitudinal grooves found posterior to tooth position 12, the medial surface dorsal to the canal is smooth. Ventral to the canal and posterior to the symphysis, the medial surface is flat and smoothly finished to the level of the thirteenth tooth position, and it is inclined slightly so that the ventral margin lies slightly lateral to the dorsal margin. At the level of the thirteenth to fourteenth tooth position, the meckelian canal expands to completely excavate the ventral half of the medial surface of the dentary posteriorly. Thus, whereas its dorsal border is well-defined by the medial surface of the dentary throughout its entire length dorsally, the canal is well-defined ventrally from the symphysis to the level of tooth 13. As in the maxilla, the alveolar shelf is shallow relative to that of other diadectids, suggesting a relatively shallow tooth implantation in the dentary.

MCZ 9438, a complete left dentary, possesses a complete tooth row, and a total of 22 teeth are present. Incomplete posteriorly, MCZ 9439 possesses the first 18 teeth of the mandibular series, and MCZ 9440 is incomplete anteriorly, possessing teeth six to 22. Such a tooth count represents the greatest yet recorded for a diadectid, with the mandibular tooth counts of other diadectids including 14 to 18 for *Diadectes* (Case 1911; Case and Williston 1912; Welles 1941; Berman et al. 1998a), 15 for

*Diasparactus* (Kissel and Lehman 2002), 14 for *Desmatodon* (Berman and Sumida 1995), 17 for *Orobates* (Berman et al. 2004), and possibly 15 for *Stephanospondylus* (Romer 1925).

MCZ 9438, MCZ 9439, and MCZ 9440 all possess a similar dental morphology In dorsal view, the dentition is aligned in the sigmoid curvature common to diadectids, but this curvature is slight and not as pronounced as in other members of the group. As in the upper jaw, the mandibular dentition of diadectids is differentiated into incisiform anterior teeth, molariform cheek teeth, and a short series of teeth intermediate to these two forms. However, whereas the anterior dentary teeth of other diadectids are strongly incisiform, those of *Ambedus pusillus* are conical; they are round in section near the base and terminate in a point, lacking the chisel-shaped, incisiform character of all other diadectids. As in other diadectids, however, the anterior dentary teeth are procumbent. Tooth 12 is the first transversely expanded tooth of the series, with teeth nine to 11 intermediate to the pointed anterior teeth and the expanded cheek teeth. The cheek teeth of the dentary possess a lesser degree of molarization than those of the maxilla (Fig. 2; Tables 1, 2) and a significantly lesser degree than the dentary cheek teeth of *Diadectes lentus*, *Diasparactus zenos*, and *Desmatodon hesperis* (Table 2). As exhibited by MCZ 9438, 9439, and 9440, they possess a low central cusp flanked by rounded shoulders both labially and lingually, not unlike those of the maxilla. In posterior view, both the labial and lingual surfaces are nearly vertical, although the lingual surface slopes medially near the base of the teeth (Fig. 2B). The teeth increase in size serially to tooth 18, from which point they slightly decrease in size posteriorly.

Nearly all of the dentary teeth possess wear surfaces, with the tips of the anterior conical teeth and the central cusp of the cheek teeth exhibiting wear. In MCZ 9439, teeth 13 to 18 are heavily worn, reducing the occlusal surfaces to smooth, flat surfaces that face dorsomedially. A smaller wear facet is present on the labial shoulder of tooth 16 in MCZ 9440. What may represent
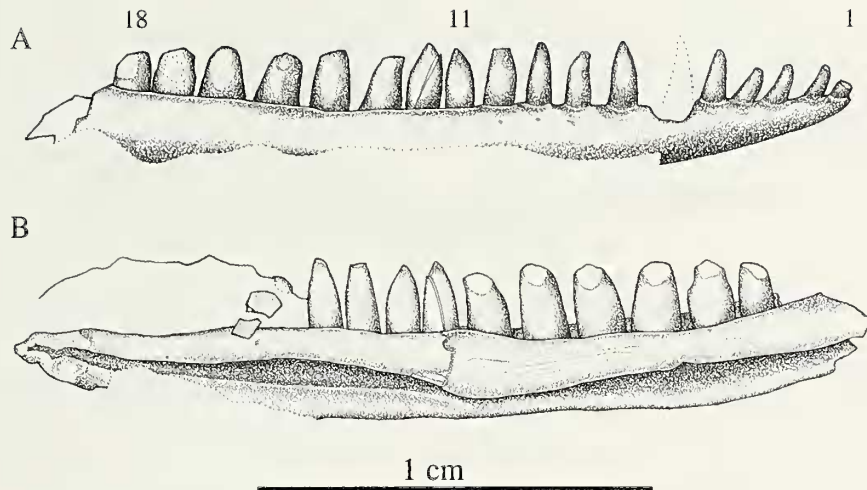
Fig. 4.—MCZ 9439, right dentary of *Ambedus pusillus* in lateral (A) and medial (B) views. Numbers indicate tooth positions.

wear facets are present on the labial shoulders of teeth 17, 18, and 21 in MCZ 9440, but these "facets" may just represent damage to the surface of the teeth. The wear pattern exhibited on teeth 13 to 18 of MCZ 9439 and tooth 16 of MCZ 9440, with a greater degree of wear on the labial cusp or shoulder of the dentary cheek teeth, is characteristic of diadectids (Berman et al. 1998b). As in the maxillary dentition, none of these wear facets possess microwear patterns that may facilitate the reconstruction of jaw movement during oral processing.

## DISCUSSION

### Ambedus pusillus *and diadectid ontogeny*

The small size of the maxilla and dentaries described herein as *Ambedus pusillus* invites the hypothesis that these elements are simply the remains of a juvenile individual of a previously described diadectid taxon, but such an interpretation is refuted by the following observations. A maxilla (CM 47668) identified as a juvenile form of *Desmatodon hesperis* possesses four dental features that are absent or greatly reduced in mature specimens of the genus and not present in specimens of *Diadectes* of any age: 1) fewer number of teeth; 2) greater relative spacing between teeth to produce large gaps between teeth; 3) first two maxillary teeth relatively longer and more incisiform; and 4) absence of wear facets (Vaughn 1972; Berman and Sumida 1995). The maxillary teeth of *Ambedus*, in contrast, outnumber those of adult *Desmatodon hesperis* specimens, they are packed tightly with little space between them, and they possess wear facets. In juvenile specimens of *Diadectes*, the cheek teeth exhibit a lesser degree of molarization than seen in the adult forms, with little or no transverse widening, a

weakly developed central cusp, and no labial or lingual cusps (Berman and Sumida 1995). Immature individuals of *Diadectes* do, however, possess a labial parapet (Berman et al. 1998a), a feature not present in *Ambedus*. Furthermore, the conical anterior dentary teeth of *A. pusillus* are distinctly different than those of *Diadectes* and *Desmatodon*, which do not exhibit any changes in their incisiform morphology throughout ontogeny (Berman and Sumida 1995).

With the understanding of diadectid ontogeny currently limited to studies of *Diadectes* and *Desmatodon* by Vaughn (1972) and Berman and Sumida (1995), comparison to immature individuals of the remaining diadectid taxa is not possible. However, in no known juvenile or adult of any diadectid taxon is the dentary as long and shallow as it is in *Ambedus*, supporting the conclusion that the material described as *Ambedus* does not represent the juvenile remains of a currently known diadectid, but rather represents a unique member of the group.

### *Phylogeny of Diadectomorpha*

Heaton (1980) proposed that Diadectomorpha represents a monophyletic group that consists of (Limnoscelidae (Tseajaiidae + Diadectidae)). Subsequent studies (e.g., Gauthier et al. 1988; Laurin and Reisz 1995, 1997, 1999; Lee and Spencer 1997) indicated that Diadectomorpha is the sister-taxon to Amniota, with Diadectomorpha + Amniota constituting Cotylosauria. However, in none of these analyses is *Tseajaia* incorporated, leaving Diadectomorpha as a monophyletic group consisting of *Limnoscelis* and diadectids. The only study since that of Heaton (1980) to consider the interrelationships of diadectomorphs is that of Berman et al. (1992). Based on a data matrix of seven taxa and nine characters of the tem-
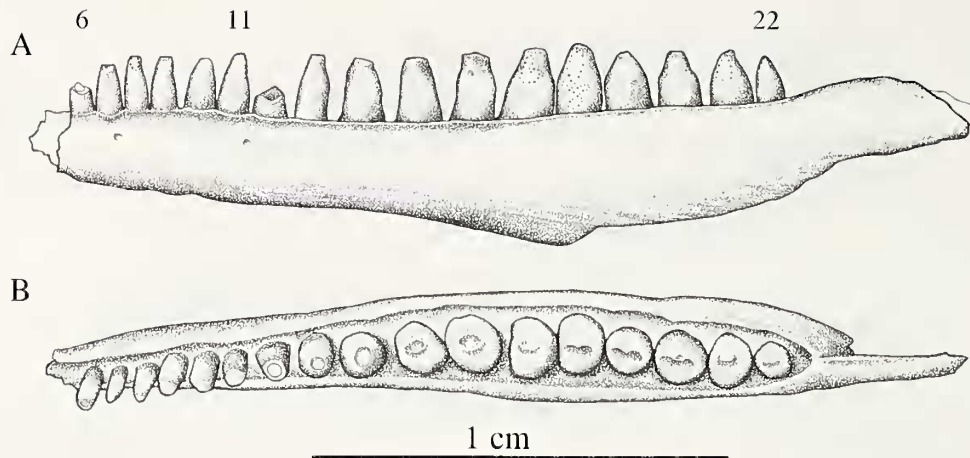
Fig. 5.—MCZ 9440, left dentary of *Ambedus pusillus* in lateral (A) and occlusal (B) views. Numbers indicate tooth positions.

poral and occipital region, the analysis of Berman et al. (1992) supported the conclusions of Heaton (1980), with Diadectomorpha consisting of (*Limnoscelis* (*Tseajaia* + *Diadectes*)).

In order to evaluate the phylogenetic position of *Ambedus pusillus*, a new phylogenetic analysis of Diadectomorpha is presented here. It includes nine taxa, including two outgroups, and 37 cranial, dental, and postcranial characters (Appendix 1, 2). Because it is incompletely known, *A. pusillus* is scored for only seven of these 37 characters; however, following the conclusions of Kearney and Clark (2003), *A. pusillus* is included in the analysis despite its incomplete nature. The analysis incorporates a number of characters that are derived from the analyses of Gauthier et al. (1988), Berman et al. (1992), Laurin and Reisz (1995, 1997), Lee and Spencer (1997), Berman et al. (1998a), and Berman (2000), but only characters that were found by these authors to possess an unambiguous history were incorporated into the current analysis. Laurin and Reisz (1997) regarded the absence of a tabular-parietal contact [24(0)] and the presence of uncinate processes [123(1)] as autapomorphies of *Diadectes*, but no specimens of *Diadectes* examined for this study possess uncinate processes, and the tabular does contact the parietal in *Diadectes*, as indicated by Berman et al. (1998a) and Berman (2000), and all diadectomorphs in which that region of the skull is known. Thus, since characters 24(0) and 123(1) of Laurin and Reisz (1997) do not represent autapomorphies of *Diadectes*, they are not included here.

Outgroups in the present analysis include Amniota, the sister-group to Diadectomorpha, and Lepospondyli. Although *Solenodonsaurus* has been found to be the sister-group to Cotylosauria (Gauthier et al. 1988; Laurin and Reisz 1999), the specimens referred to that genus are

fragmentary and lack much anatomical information; thus, Lepospondyli, the sister-taxon to *Solenodonsaurus* + Cotylosauria, was selected as the second outgroup. Within Diadectomorpha, *Limnoscelis*, *Tseajaia*, *Ambedus*, *Orobates*, *Desmatodon*, *Diasparactus*, and *Diadectes* were analyzed. Due to their incomplete nature and uncertain affinities, *Phanerosaurus*, *Stephanospondylus*, and the Richards Spur diadectid(s) were not included in the analysis. Since *Tseajaia* remains the only genus assigned to Tseajaiidae, and all limnoscelids have been referred to the genus *Limnoscelis* (Wideman 2002), both Tseajaiidae and Limnoscelidae represent monogeneric taxa, so the nomina Limnoscelidae and Tseajaiidae are therefore abandoned.

Using Paup 4.0b10 (branch and bound search; Swofford 2002) and MacClade 4.0 (Maddison and Maddison 2000), the analysis yielded a single most parsimonious tree with a length of 53 steps, a consistency index (CI) of 0.8491, and a retention index (RI) of 0.8261. The resulting tree (Fig. 6) supports the previous hypothesis that *Limnoscelis*, *Tseajaia*, and diadectids form a monophyletic group, with diadectids and *Tseajaia* sharing a more recent common ancestor than either does with *Limnoscelis*. The monophyly of Diadectidae is also supported, with diadectids consisting of a series of nested clades that terminates with *Diasparactus* + *Diadectes*. Diadectidae is defined here as *Diadectes* and all taxa sharing a more recent common ancestor with *Diadectes* than with *Tseajaia*.

*Ambedus* is found to be the sister-taxon to all other members of Diadectidae. Although the known remains of *Ambedus* lack many of the structures considered in the analysis, the absence of a labial parapet of the dentary, deep tooth implantation, deep lower jaw, and well-developed molariform teeth with lateral and lingual cusps

supports the position of *Ambedus* as the sister-taxon to all other diadectids.

Node E is diagnosed by the presence of a labial parapet of the dentary [22(1)], the presence of marginal teeth with roots longer than the height of the crown [26(2)], and the presence of incisiform anterior teeth [28(1)]; node F is diagnosed by the presence of a secondary palatal shelf [12(1)] and the presence of a deep lower jaw [20(1)]; and node G is diagnosed by the presence of a jaw articulation located ventral the occlusal plane [19(1)], the presence of a tall labial parapet [22(2)], the presence of a high degree of molarization of the cheek teeth [30(2)], and the presence of well-developed labial and lingual cusps of the cheek teeth [31(2)]. Thus, the phylogeny of Diadectidae presented here suggests that a trend toward more efficient oral processing characterizes the evolutionary history of the group. The labial parapet of the dentary may have supported a beak (Welles 1941), served as a masticatory surface for the labial margins of the maxillary cheek teeth (Berman et al. 1998b), or both; the secondary palatal shelf may have provided an occlusal surface for the dentary cheek teeth (Olson 1947; Berman et al. 1998b); and a massive lower jaw, the depression of the jaw joint relative to the occlusal plane, and transversely expanded cheek teeth are three skeletal features indicative of herbivory (Olson et al. 1991; Hotton et al. 1997; Sues and Reisz 1998; Reisz and Sues 2000).

As previously stated, the analyses of Gauthier et al. (1988), Laurin and Reisz (1995, 1997, 1999), and Lee and Spencer (1997) hypothesized that Amniota and Diadectomorpha are sister-taxa. Berman et al. (1992) and Berman (2000) concluded differently, suggesting that Synapsida is the sister-taxon to Diadectomorpha. This latter hypothesis, due to its unconventional nature, deserves consideration here. Berman et al. (1992) united synapsids and diadectomorphs based on the presence of three synapomorphies: 2(1), posterolateral corner of the skull table formed entirely or nearly entirely by the supratemporal; 3(1), long posterior expansion of postorbital contacts supratemporal to exclude the parietal lappet from contacting the squamosal; and 5(1), possession of an otic trough. These characters are problematic. Although character state 2(1) is present in early synapsids, recently described remains of *Diadectes* indicate that the posterolateral corner of the skull table of *Diadectes* is formed subequally by the supratemporal and tabular (Berman et al. 1998a), a condition shared with all other diadectids in which this region of the skull is known, *Desmatodon* (Vaughn 1972; fig. 4) and *Orobates* (Berman et al. 2004). As evidenced by YPM 811, the holotype of *Limnoscelis paludis*, the type species of the genus, the posterolateral corner of the skull table of *Limnoscelis* is also characterized by near equal contributions of the supratemporal and tabular. Only in *Tseajaia* does the tabular only contribute slightly to the posterolateral corner of the skull table, with

the supratemporal representing the dominant element of the region (Moss 1972). Thus, the presence of a skull table in which the posterolateral corner is formed entirely or nearly entirely by the supratemporal [7(1) of the present study] is not shared by synapsids and all diadectomorphs, and its presence in *Tseajaia* and synapsids may represent a convergence. As indicated by Laurin and Reisz (1995), the second character [3(1)] of Berman et al. (1992) is present in diadectomorphs and all of Amniota, whereas the third [5(1)] may have evolved convergently in both diadectomorphs and Synapsida, since several early synapsids (e.g., *Eothyris*, *Varanops*, and *Aerosaurus*) have no otic trough.

Based on an analysis of eight characters of the occipital region, Berman (2000) cited the following three synapomorphies to link diadectomorphs and synapsids: 5(2), a deep, nonsculptured component of the tabular contacts the distal end of a ventrally displaced, laterally directed paroccipital process, enclosing laterally a small, ventrally displaced, posttemporal fenestra; 6(1), presence of an otic trough of the opisthotic; and 7(1), posterolateral corner of the skull table is formed subequally by the supratemporal and the tabular. As indicated by Berman (2000), character state 7(1) represents a modification of character state 2(1) of Berman et al. (1992), with the other two states (0, posterolateral corner of the skull table formed entirely by the tabular; and 2, posterolateral corner of the skull table formed almost entirely by the parietal and partly by a greatly reduced supratemporal) of characters 7 and 2 remaining identical. The posterolateral corner of the skull table in all diadectomorphs except *Tseajaia*, as discussed above, is indeed formed subequally by the supratemporal and tabular, but that of synapsids is formed entirely or nearly entirely by the supratemporal. Thus, whereas Diadectomorpha was incorrectly coded for character 2 of Berman et al. (1992), it is properly coded for character 7 of Berman (2000), and whereas Synapsida was correctly coded for character 2 of Berman et al. (1992), it is incorrectly coded for character 7 of Berman (2000). Character states 7(1) and 2(1) of Berman (2000) and Berman et al. (1992) can therefore not be regarded as a synapomorphy uniting Diadectomorpha and Synapsida.

The second character state [6(1)] of Berman (2000) to link diadectomorphs to synapsids was refuted by Laurin and Reisz (1995) after its first description by Berman et al. [1992; 5(1)], as indicated above, and the first character [5(2)] is also questionable. Examination of YPM 811 indicates that the tabular of *Limnoscelis* does not contact the paroccipital process of the opisthotic to enclose a small posttemporal fenestra (*contra* Berman 2000). The occipital regions of UCMP 59012, the holotype of Tseajaia campi, and FMNH UC 675, the only specimen of *Diasparactus* to possess the skull, are imperfectly preserved, leaving the relationship between the tabular and opisthotic uncertain in both taxa. Although Vaughn (1972; fig. 4) described the presence of a fenes-
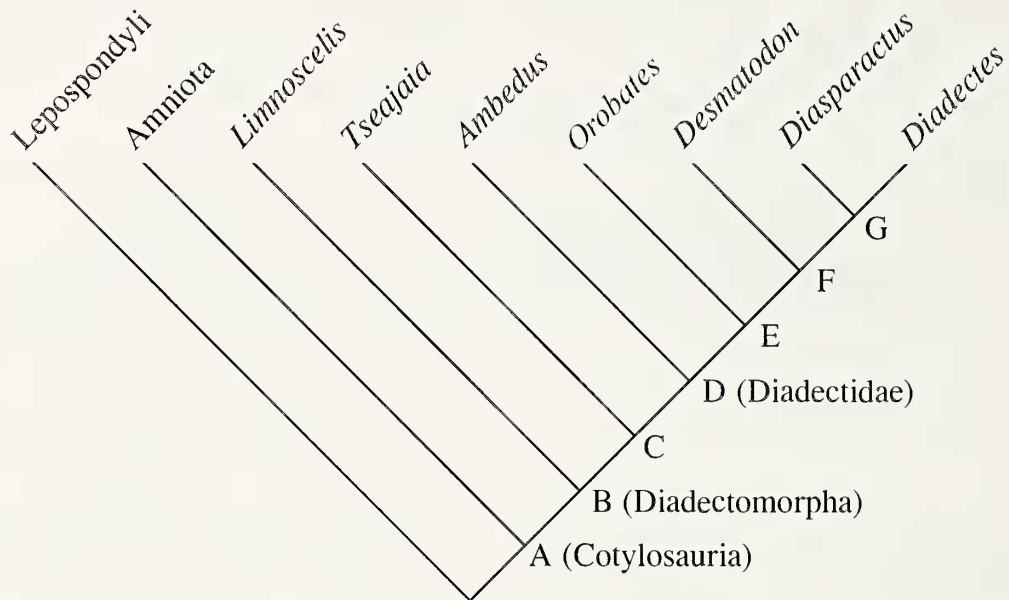
Fig. 6.—Hypothesis of diadectomorph interrelationships. Autapomorphies of the clades and terminal taxa are as follows, with all characters listed possessing an unambiguous history: Node A (Cotylosauria): 5(1), 33(1), 35(1); Amniota: 1(1), 11(1), 24(1); Node B (Diadectomorpha): 2(1), 4(1), 18(1), 25(1), 26(1), 32(1), 36(1), 37(1); Node C: 3(1), 8(1); Node D (Diadectidae): 27(1), 30(1), 31(1); Node E: 22(1), 26(2), 28(1); Node F: 12(1); 20(1); Node G: 19(1), 22(2), 30(2), 31(2).

tra between the postparietal and tabular in *Desmatodon hesperis*, no fenestra is located between the tabular and opisthotic. Thus, if Berman's (2000) interpretation of the occipital region of *Diadectes* is correct, then the presence of character [5(2)] in *Diadectes* and some synapsids is likely the result of convergence.

With most of the characters used by Berman et al. (1992) and Berman (2000) to link diadectomorphs and synapsids either refuted or in question, the recognition of diadectomorphs and synapsids as sister-taxa is not well supported. Rather, based on the more inclusive analyses performed by Gauthier et al. (1988), Laurin and Reisz (1995, 1997, 1999), and Lee and Spencer (1997), which employed much larger data matrices than those of Berman et al. (1998) and Berman (2000), Diadectomorpha is regarded as the sister-taxon to Amniota, not a member of it.

CONCLUSIONS

Phylogenetic analysis supports previous hypotheses that *Limnoscelis*, *Tseajaia*, and Diadectidae form a monophyletic group (Diadectomorpha), with diadectids and *Tseajaia* sharing a more recent common ancestor than either does with *Limnoscelis*. This analysis is the first to

consider the interrelationships of Diadectidae, which was found to represent a monophyletic group consisting of (*Ambedus* (*Orobates* (*Desmatodon* (*Diasparactus* + *Diadectes*)))). Inclusion of more data will further test this hypothesis of relationships.

The description of *Ambedus pusillus* increases the total number of currently recognized diadectid taxa to seven genera and thirteen species: *Diadectes sideropelicus* Cope 1878; *Diadectes tenuitectes* (Cope 1896); *Diadectes lentus* (Marsh 1878); *Diadectes carinatus* (Case and Williston 1912); *Diadectes sanmiguelensis* Lewis and Vaughn 1965; *Diadectes absitus* Berman et al. 1998a; *Diasparactus zenos* Case, 1910; *Desmatodon hollandi* Case, 1908; *Desmatodon hesperis* Vaughn, 1969; *Phanerosaurus naumanni* Meyer, 1860; *Stephanospondylus pugnax* (Geinitz and Deichmüller 1882); *Orobates pabsti* Berman et al., 2004; and *Ambedus pusillus*. As previously indicated, the affinity of the diadectid remains from Richards Spur are uncertain at this time. With the recognition of Limnoscelidae as a monogeneric taxon (Wideman 2002), the Permo-Carboniferous clade Diadectomorpha consists of (*Limnoscelis* (*Tseajaia* + Diadectidae)) (Fig. 6). Only two species of *Limnoscelis*, *L. paludis* Williston, 1911 and *L. dynatis* Berman and Sumida, 1990, are currently recog-

nized, and *Tseajaia* is a monospecific genus, with *T. campi* Vaughn, 1964 as its only member. Thus, if the number of species associated with sister-taxa Diadectidae and Tseajaia is considered, it is found that members of Diadectidae constitute the majority of species within that clade, an asymmetry of species-richness that suggests an evolutionary radiation of Diadectidae.

Based on cranial, dental, and postcranial anatomy, members of Diadectidae are thought to represent the earliest known examples of vertebrates capable of processing a diet of high-fiber terrestrial plants (Hotton et al. 1997; Sues and Reisz 1998; Reisz and Sues 2000). As the first terrestrial vertebrate herbivores, diadectids inhabited previously unoccupied ecological space. It is therefore hypothesized that the evolution of high-fiber herbivory in Diadectidae led to the radiation of species within that group, producing a clade that is markedly more species-rich than other diadectomorph taxa. *Ambedus pusillus* is unique among diadectids in its high maxillary and mandibular tooth counts, lack of incisiform anterior teeth, shallow dentary, lack of a labial parapet, relatively shallow alveolar shelf suggesting the presence of teeth with roots shorter than the height of the crown, and lesser degree of molarization of the cheek teeth. Despite lacking a deep lower jaw, which is characteristic of herbivores and found in other diadectids, the presence of procumbent anterior teeth, molariform cheek teeth, and wear facets similar to those of other diadectids suggest that *Ambedus*, like all other diadectids, may have been herbivorous. However, in the absence of additional material, such as postcranial and more complete skull remains, it is not possible to determine if *Ambedus* was a high-fiber herbivore, and it is therefore not possible to determine if the acquisition of high-fiber herbivory evolved within Diadectidae. In addition, with the validity of several diadectid species in question (e.g., *Phanerosaurus naumanni* and *Stephanospondylus pugnax*; Berman et al. 1998a), further evaluation of diadectid phylogeny and patterns of diadectid temporal and geographic distribution are required before the evolutionary history of Diadectidae is resolved.

## ACKNOWLEDGMENTS

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TABLE 1. *Maximum crown measurements (in mm) and ratios of largest preserved, midseries maxillary cheek teeth in selected specimens of* Diadectes, Desmatodon, Orobates, *and* Ambedus. *Modified from Berman and Sumida (1995).*

| | Maximum transverse width | Maximum anteroposterior length | Maximum height | Length/Width | Height/Width |
|---|---|---|---|---|---|
| *Diadectes lentus*<br>FMNH UC 675 (positions 6 to 8) | 13.6 | 5.3 | 5.5 | 0.39 | 0.40 |
| *Desmatodon hesperis*<br>CM 47654 (holotype; positions 7 and 8); CM 47677 seventh posteriormost preserved tooth) | 7.8; 9.3 | 5.3; 4.5 | 8.5; 8.0 | 0.68; 0.48 | 1.09; 0.86 |
| *Desmatodon hollandi*<br>CM 1938 (holotype; ?eighth posteriormost preserved tooth) | 9.5 | 4.3 | 7.0 | 0.45 | 0.74 |
| *Desmatodon aff. D. hollandi*<br>YPM 8639 (CM 38044; positions 9 to 11) | 9.5 | 4.3 | 7.0 | 0.45 | 0.74 |
| *Orobates pabsti*<br>MNG 11134 (positions 6 to 8) | 5.4 | 1.8 | 6.0 | 0.33 | 1.11 |
| *Ambedus pusillus*<br>MCZ 9436 (holotype; tooth 9; tooth 8) | 2.11; 1.94 | 1.06; 1.10 | 1.86; 1.91 | 0.50; 0.57 | 0.88; 0.99 |

TABLE 2. *Maximum crown measurements (in mm) and ratios of largest preserved, midseries dentary cheek teeth in selected specimens of* Diadectes, Desmatodon, Orobates, *and* Ambedus. *Modified from Berman and Sumida (1995) and Kissel and Lehman (2002).*

| | Maximum transverse width | Maximum anteroposterior length | Maximum height | Length/Width | Height/Width |
|---|---|---|---|---|---|
| *Diadectes lentus*<br>FMNH UC 675 (probable positions 8 to 10) | 11.6 | 4.7 | 5.5 | 0.41 | 0.47 |
| *Diasparactus zenos*<br>OMNH 55350 (tooth 10) | 13.0 | 5.0 | 5.5 | 0.38 | 0.42 |
| *Desmatodon hesperis*<br>CM 47670 (positions 9 to 11); CM 47661 (isolated crown) | 8.8; 10.5 | 4.7; 5.7 | 7.0; 6.8 | 0.53; 0.54 | 0.80; 0.65 |
| *Orobates pabsti*<br>MNG 11134 (tooth 14) | 5.3 | 2.7 | 6.4 | 0.51 | 1.21 |
| *Ambedus pusillus*<br>MCZ 9440 (sixth posteriormost tooth position; fifth posteriormost tooth position) | 1.35; 1.35 | 1.10; 1.01 | 1.69; 1.69 | 0.82; 0.75 | 1.3; 1.3 |

1) Frontal: excluded from orbit (0); contacts orbit between prefrontal and postfrontal (1). (Laurin and Reisz 1997, 8).

2) Lateral parietal lappet: absent (0); present (1).

3) Parietal foramen diameter: less than 33% (0) or 33% or greater than the anteroposterior length of the parietal midline suture (1).

4) Postparietal: paired (0); single and median (1). (modified from Laurin and Reisz 1995, 4; Laurin and Reisz 1997, 22).

5) Postparietal position: on skull table or on skull table and occiput (0); only on occiput (1). (Laurin and Reisz 1997, 23; Lee and Spencer 1997, 11).

6) Tabular: large, on skull table and occiput (0); reduced, on skull table and occiput (1); reduced, nearly to entirely occipital (2).

7) Posterolateral corner of skull table: formed entirely by tabular (0); formed entirely or nearly entirely by supratemporal (1); formed subequally by the supratemporal and tabular (2). (modified from Berman et al. 1992, 2; Berman 2000, 7).

8) Vertical, shallow temporal notch: absent (0); present (1).

9) Internal nares: short (0); long, where the ratio of the anteroposterior length of the internal nares to the length of the skull table 33% or greater (1).

10) Denticles on palate: present (0); absent (1). (Laurin and Reisz 1997, 53).

11) Three distinct rows of teeth on palate: absent (0); present (1).

12) Secondary palatal shelf formed by palatine and ectopterygoid: absent (0); present (1).

13) Palatal ramus of pterygoid makes substantial contribution to posterior medial border of internal naris and prevents a palatine-vomer contact: absent (0); present (1). (Berman et al. 1998a).

14) Medial row of teeth on palatal ramus of pterygoid: absent (0); present (1).

15) Transverse flange of pterygoid: lies at approximately the same level as the palate (0); projects ventrally to or below the level of the maxillary dentition (1).

16) Well-developed teeth on the margin of the transverse flange of the pterygoid: absent (0); present (1).

17) Contact between supratemporal and the dorsal margin of the paroccipital process of opisthotic: absent (0); present (1). (Berman et al. 1998a)

18) Otic trough in ventral flange of opisthotic: absent (0); present (1). (Laurin and Reisz 1995, 58).

19) Position of jaw articulation: at approximately the same level as the occlusal plane (0); ventral to the occlusal plane (1).

20) Deep lower jaw: absent (0); present, where the ratio of the dorsoventral height of the mandible at the level of the coronoid eminence to the anteroposterior length of the jaw is 33% or greater (1). With the exception of *Diadectes absitus*, all species of *Diadectes* possess a deep lower jaw. Because of this and other features detailed by Berman et al. (1998a), the diadectid specimens described as *D. absitus* are quite distinct from those of North American *Diadectes* species. These differences suggest the need to reexamine the specimens described as *D. absitus* and their

assignment to the genus *Diadectes*, but until this issue is explored by the current authors with a detailed phylogenetic analysis of Diadectidae, *D. absitus* is recognized herein, and the genus of *Diadectes* is coded as possessing a deep lower jaw. If future analyses support the inclusion of this material into the genus *Diadectes*, then the shallow lower jaw in *D. absitus* is likely an autapomorphy of that form, as indicated by Berman et al. (1998a).

21) Meckelian fenestra: absent (0); elongate (1); tall, where the ratio of the greatest dorsoventral height to the anteroposterior length is 25% or greater (2).

22) Labial parapet: absent (0); low, where the parapet never projects higher than the bases of the cheek teeth (1); tall, where the parapet is as tall or taller than the occlusal surface of the teeth near the posterior end of the tooth row (2). This character, like 20, is problematic within the genus *Diadectes*. All examined specimens of *Diadectes* recovered from North America possess a tall labial parapet, but those from Germany described as *Diadectes absitus* possess a low labial parapet. As indicated in the discussion of character 20, the taxonomic status of *D. absitus* will be examined in order to further resolve this issue.

23) Anterior process of articular: absent (0); present (1).

24) Coronoid teeth: present (0); absent (1).

25) Infolding of dentine: absent (0); present (1). (Gauthier et al.1988, 44; Laurin and Reisz 1995, 68).

26) Deep marginal tooth roots: absent (0); present, with root length less than crown height (1); present, with root length greater than crown height (2).

27) Heterodont dentition, characterized by the presence of transversely expanded cheek teeth: absent (0); present (1).

28) Anterior teeth: conical (0); incisiform (1).

29) Procumbent anterior teeth: absent (0); present in the lower jaw only (1); or present in both upper and lower jaws (2).

30) Degree of molarization of largest preserved, midseries dentary cheek teeth: absent (0); low (1); high, where the degree of molarization is considered high if the ratio of anteroposterior length to mediolateral width and dorsoventral height to mediolateral width are both less than 0.50 (2).

31) Labial and lingual cusps of cheek teeth: absent (0); weakly developed, represented by shoulders (1); or well developed (2).

32) Anterior process of axial intercentrum-atlantal pleurocentrum complex: absent (0); present (1). (Sumida et al. 1992, 9; Laurin and Reisz 1995, 84; Laurin and Reisz 1997, 111).

33) Neural arches of dorsal vertebrae: flat or concave (0); swollen (1). (Laurin and Reisz 1997, 107; Sumida and Modesto 2001).

34) Neural spines: short (0); tall, where the ratio of neural spine height to vertebral height is greater than 40% (1).

35) Sacrum composed of one (0), or at least two (1) vertebrae. (Gauthier et al. 1998, 65; Laurin and Reisz 1997, 119).

36) Lateral shelf on iliac blade: absent (0); present (1). (Heaton 1980; Laurin and Reisz 1995, 107).

37) Humerus with a distinct shaft (0), or short and robust, without a distinct shaft (1). (modified from Laurin and Reisz 1995, 104).

APPENDIX 2. *Data matrix used in this study.*

| Taxon | 1 2 3 4 5 6 7 8 9 1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 2 2 2 2 2 3 3 3 3 3 3 3<br>0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 |
|---|---|
| Lepospondyli | 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 |
| Amniota | 1 0 0 0 1 2 1 0 0 0 1 0 0 1 1 1 0 0 0 0 0 0 1 0 0 0 0 0 0 0 1 0 1 0 0 |
| *Limnoscelis* | 0 1 0 1 1 1 2 0 1 0 0 0 0 0 1 1 0 1 0 0 1 0 0 0 1 1 0 0 0 0 0 1 1 0 1 1 1 |
| *Tseajaia* | 0 1 1 1 1 1 1 1 1 0 0 0 0 1 0 0 ? 1 0 0 2 0 0 0 1 1 0 0 0 0 0 1 1 0 1 1 1 |
| *Ambedus* | ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? ? 0 ? 0 ? ? 1 1 0 ? 1 1 ? ? ? ? ? ? |
| *Orobates* | 0 1 1 1 1 1 2 1 ? 0 0 0 ? 1 0 0 1 1 0 0 2 1 0 1 1 2 1 1 1 1 1 1 1 0 1 1 1 |
| *Desmatodon* | ? 1 1 1 1 1 2 1 ? 0 0 1 ? 1 1 0 1 1 0 1 2 1 1 1 1 2 1 1 1 1 1 ? 1 1 ? ? 1 |
| *Diasparactus* | ? ? 1 ? ? ? ? ? ? ? 1 ? ? ? ? ? ? 1 1 ? 2 ? ? 1 2 1 ? ? 2 2 1 1 1 1 1 1 |
| *Diadectes* | 0 1 1 1 1 1 2 1 0 1 0 1 1 1 0 1 1 1 0 1 1 1 2 2 1 1 1 2 1 1 2 2 2 1 1 0 1 1 1 |